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The Role of Fungi in Weed Biocontrol: A Review

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Abstract

Weeds are one of the major threats to the agricultural sector as well as to the natural environment, and it is important to control them. They cause serious threats to commercial crop production, global vegetation, and human health. Invasion by exotic weed species imposes a significant impact on native plant communities and their biodiversity, leading to major changes in global vegetation patterns. Biological control has become popular during the past few decades. In agricultural systems, weeds are controlled using chemicals. However, it has some limitations in natural systems. Furthermore, the use of biological control for weeds increased due to increased public awareness of the negative impacts of chemical herbicides and the increase of herbicide-resistant weeds. Biological control of weeds focuses on the use of co-evolved natural enemies such as fungi, bacteria, and viruses. Nowadays, biological control of weeds with fungi was popular because it is environmentally safe, sustainable and has beneficial applications. This review focuses on fungi as potential biocontrol agents for weeds and the success achieved in case studies.

Keywords – invasive weeds – mycoherbicides – natural enemies – weed management

Introduction

Weed is a plant that reduces the agricultural production and the environmental or aesthetic value of the land, according to Popay (2008). Merriam-Webster (2021) defined a weed as “a plant that is not valued on where it is growing and is usually of vigorous growth”. Weeds can be categorized into three types, annuals, biennials and perennials (Tilley 2019). Plant families with the highest number of weeds are Asteraceae, Poaceae, Fabaceae and Brassicaceae (Onen et al. 2018). Weeds require nutrients, water and sunlight for their survival and also compete for space with crop plants. The more intense their competition is more damage is caused to the crop yield. Factors that affect weed-crop competition are the timing of weed emergence, their growth form, weed density, and characteristics of weed and crop species (Hasanuzzaman 2015).

Weeds that can establish, persist and widely spread in natural ecosystems outside the plant’s native range are called invasive weeds (Randall 1997). Invasive weeds also decrease the quality or cause toxicity to livestock. One of the well-known examples is fireweed. It contains pyrrolizidine alkaloids, which cause liver damage in livestock, in severe cases, increase mortality (Gardner et al. 2006).

Invasive weeds also affect the natural environment. They can change the balance of ecological communities and their diversity. Weeds invade native plants by posing a threat to

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biodiversity (Coutts-Smith & Downey 2006). They also destroy native habitats and ecosystems, including rivers and forests. Losses caused by invasive weeds are economically more harmful than other crop pests (Gharde et al. 2018). According to Gharde et al. (2018), weeds cause loss to the economies in many countries. For example, it was reported to cost about US$ 11 billion for ten major field crops in 18 states of India (Gharde et al. 2018).

As a consequence, many scientists are finding strategies for weed control. Traditional weed management involves practices adopted by farmers to reduce weed problems in agriculture. Cultural practices to control weeds include crop rotation, mulching, hand pulling, tillage operation, and hoeing (Shrestha 2006, Heap 2014, Leghari et al. 2015). Hoeing with hands and deep tillage operation apply to all crops. Although some weeds cannot be controlled completely by chemicals and herbicides (Heap 2014), deep tillage operation can destroy weeds by inhibiting the germination and establishment of the weed (Shrestha 2006).

The application of herbicides is one of the solutions to control weeds on agricultural lands. Although it is an effective method, it damages the environment, and the remaining toxic herbicide residues concentrate in groundwater, soil and animals, ultimately passed to human food chains (Torretta et al. 2018). The evolution of herbicide-resistant weeds is another problem caused by excessive herbicide usage, and up to now, 263 different weed species are resistant to herbicides (Heap 2021).

The current trend of weed management focuses on finding new approaches instead of applying chemical herbicides and traditional cultural practices (Labrada 2003, Gnanavel 2015, Harms et al. 2021, Whelan 2021). Some environmental-friendly and effective methods have been applied in weed control, such as intercropping, biological control, use of bio-herbicides and cultural control over weed communities (Gnanavel 2015). In the case of biological control, bacteria, fungi, virus, and insects have been applied successfully during weed control.

In the 1970s, Paterson’s curse, the most widespread and toxic broadleaved agricultural weed, has been successfully controlled in Australia (Sheppard et al. 2002). Field release of rust fungus (*Puccinia myrsiphylli*) and leafhopper (Tribe *Erythroneurini*) controlled the bridal creeper in 1999 and 2000. *Puccinia chondrillina* is considered the most successful program for the biocontrol of skeleton weed. After 2005, skeleton weed was no longer considered a serious threat to cropping areas in southeast Australia (CSIRO 2017). This program increased crop yield, reduced herbicide usage and saved over US$12 million annually. The current review discussed two main ideas, the classical approach (introducing exotic organisms) and the inundative approach (treating weeds by increasing the mycoherbicide inoculum amount). We also emphasized the usage of fungi as a biocontrol agent by providing some successful examples.

Current methods used in weed control

Weeds harm both crops and human health. They cause problems in many parts of the world. Therefore, weed scientists are continuously seeking strategies to control weeds. Nowadays, there are three major categories in weed management, cultural controlling method, chemical controlling method, and biological controlling method. Cultural methods are traditional and widely adopted by farmers in crop production to reduce weed interference. It includes crop rotation, crop competition, planting time, and cultivar selection (Shrestha 2006, Heap 2014, Leghari et al. 2015). These methods are accepted because of their environmental friendliness and cost-effectiveness (Upadhyaya & Blackshaw 2007). As the famous saying “Prevention is better than cure”, most cultural methods focus on avoiding weed establishment by preventing their spread in the field. Most of these were performed manually using hands, tools, or machines. These practices include physical removal of weeds by grazing, burning, mowing, mulching, tilling, or hand removal (Sahin 2019, Tang et al. 2021, GlobalNet Academy 2021). There are many advantages as well as disadvantages to each method. For example, mechanical weed control provides many benefits to soil, but those pieces of equipment and machines used in one area will become a vector for weed seeds spreading to another (Randall 2016). After using the machines and tools in weed control, it is always important to properly clean them, vehicles, or even footwear (free of weed seed) to avoid their spread into un-infested sites (Gill et al. 2018). These cultural control methods aim to reduce weed pressure but are limited by the high-cost implementation, skilled labour, and unavailability of equipment (Norsworthy et al. 2012).

Chemical herbicides successfully control weed populations by reducing labour demands (Gianessi 2009). In chemical control, herbicides play an important role in inhibiting the growth of weeds. This method is useful in commercial operations (Kraehmer et al. 2014). Herbicides are classified into two categories according to their control action; selective herbicides (kill only targeted weeds) and non-selective herbicides (kill all the surrounding vegetation) (Vats 2015). Several chemical families are composed of active ingredients for herbicide production. Forouzesh et al. (2015) described over 400 active ingredients belonging to various chemical families and also provided the systematic classification and mechanism of action of these metabolites. Glyphosate glycine is one of the most-used herbicides in agriculture (Duke & Powles 2008, Soumis 2018, Duke 2020). It is a non-selective, broad-spectrum, organophosphorus herbicide that targets weeds, grasses, and woody plants, causing an impact on the environment (Defarge et al. 2018, Soumis 2018, Duke 2020). As a consequence of using excessive herbicides, some weeds become resistant and no longer respond to herbicides. For example, populations of horseweed (Conyza canadensis (L) Cronq) are resistant to N-(phosphonomethyl)glycine (Owen & Zelaya 2005). When glyphosate is applied to weeds annually, the weed species become naturally tolerant to glyphosate within 5-8 years (Madsen 1994). Further, some herbicides cause health problems in humans, such as cancer, respiratory problems, and reproductive and developmental changes (Marin-Morales et al. 2013). Another adverse effect of using chemical herbicides is the herbicide residues that remain in the environment. This seriously threatens the future of agriculture and damages the natural environment (Ahlgren 2004). For instance, glyphosate has a high risk of contaminating groundwater with its metabolites residues in the long term (Al-Rajab & Hakami 2014). When these residues concentrate at higher levels in natural food chains, people may indirectly ingest them influencing human health and natural biodiversity (Zia et al. 2009). Soil microflora (some bacteria and fungi) are also sensitive to the persistence of glyphosate and its metabolites in soil. (Duke et al. 2012). For example, soil microbial respiration (SMR) and soil microbial biomass (SMB) were strongly influenced by glyphosate concentration depending on the dose and time of herbicide application (Nguyen et al. 2016).

However, many farmers rely on these chemical herbicides because of their effectiveness in a relatively short time. It is still considered an efficient method for weed control. The application of these methods in the past has shown that integrating one or more chemical and cultural practices is more effective and economically beneficial than applying only one approach (Harker & O’Donovan 2013, Swanton & Murphy 1996).

Because of the facts that we mentioned above, researchers are trying advanced technologies for weed management. These approaches are new and non-traditional and integrate techniques, such as genetic engineering, infrared radiation, microwave radiation, electronic weed control, and ultrasonic weed control systems in their strategies (Harms et al. 2021, Whelan 2021).

Biocontrol as an alternative method for weed control

Biocontrol is emerging as an alternative for successful weed control. There have been many challenges to the successful use of this method and involved new techniques and knowledge (Boyetchko & Peng 2004, Dagno et al. 2012, Kumar et al. 2021). Biocontrol of weed is being adopted in recent times because it is a green alternative to chemicals (Sharma et al. 2017). Biocontrol involves the use of living organisms (bacteria, viruses, fungi, and insects) to control or reduce weed communities (Harding & Raizada 2015, Petit & Bohan 2018). Most organisms used for this are either parasites, pathogens or predators, which can be harmful to weed survival. Among them, microorganisms are the most abundant group used in weed biocontrol (Kennedy 2019). This method is considered effective and does not cause any damage to the environment (Sharma et al. 2017).

Biocontrol mechanism for weeds

Similar to higher plants, weeds also have structural and chemical defenses to prevent invading organisms before causing extensive damage to the plant (Freeman & Beattie 2008). The pre-formed structural defenses are waxy cuticles and cellulose cell walls. During plant-pathogen interaction, the more permeable cuticle is, the more favorable or susceptible to pathogenic infections (Ziv et al. 2018). The plant cell wall has several important functions for the survival of the whole plant. When the pathogen contacts the host plant, plants resist external penetration by several pre-formed barriers.

Pathogens are categorized into three types depending on their lifestyles: biotrophs, hemibiotrophs and necrotrophs (Freeman & Beattie 2008, Doehlemann et al. 2017, Tronsmo et al. 2020, Trapet et al. 2021). Hemibiotrophic fungi have both biotrophic and necrotrophic strategies (Perfect & Green 2001). Most fungal biocontrol agents are hemibiotrophs because they provide high specificity during biotrophic growth and cause weed death during the subsequent necrotrophic growth (Goodwin 2001). In the initial biotrophic stage, the host immune system is suppressed by allowing invasive hyphae to enter the host tissues. The second stage of infection is processed by necrotrophic action. In this stage, harmful toxins are secreted by pathogens and eventually cause the death of the host plant (Koeck et al. 2011).

In plants, we can mainly find three types of pathogenic organisms, fungi, bacteria and viruses. We will give a brief review of the infection process of those organisms. The fungal infection process is initiated when they attach to the host plants. After the fungal spores are germinated, fungi develop attachment structures called appressoria that penetrate the epidermal cells and form haustoria to absorb nutrients from the host (Bushnell 1972, Mendgen & Hahn 2002, Kemen et al. 2005, Pawlowski & Hartman 2016). In necrotrophic fungi, the appressoria excrete phytotoxins and enzymes to degrade pre-existing structural defenses, such as plant cuticles and cell walls. Those enzymes and phytotoxins can kill plant cells, cause necrotic lesions, and sometimes cause plant death (Pawlowski & Hartman 2016). However, spore germs of phytopathogenic fungi do not form appressoria on leaves with removed cuticles or in vitro because the development of appressoria is stimulated by cuticular wax (Dyakov et al. 2007).

Many plant viruses transmitted by insect vectors and insects create an entry point for them (Asher 2018). Sometimes viruses can enter through the wounded cells of plants (Garcia-Ruiz 2019). A virus requires a living host to grow and multiply. When a virus infects plants, they carry the genetic materials to control the host cell’s machinery and produce proteins and new viruses. RNA silencing is an antiviral defense mechanism of plants. Viral genetic material is recognized by plant cells through RNA silencing so that the other cells can be informed to kill the virus. However, viruses survive in plants by suppressing RNA silencing. The strategy to overcome RNA silencing is to produce suppressor proteins that can block the host silencing pathway and interfere with its function in plant cells. For example, the V_2 suppressor protein blocks the plant’s RNA silencing (Sheikh 2018).

Bacteria produce several virulence factors to promote their growth and cause diseases in plants (Tripathi 2017). In their infection process, bacteria import virulence proteins into the plant’s apoplast or cytoplasm. There are three protein secretion pathways, type 2, type 3 and type 4 secretion systems (Van Gijsegem et al. 1993, Green & Mecsas 2016). Among them, the type 3 protein secretion system is the most widely studied. The type 3 secretion system is related to bacteria flagellum. A pilus (hair-like appendage) injects the effectors or virulence proteins into the plant cells (Lindberg et al. 1987). Effectors promote the virulence of the bacterial pathogen by affecting the enzymatic activities of ubiquitin-like proteases, proteases, E3 ubiquitin ligases, cysteines and protein phosphatases. The bacterial toxins (coronatine, tabtoxin, phaseolotoxin) are important for virulence and symptom development (Abramovitch et al. 2006).

Potential biocontrol agents

Understanding the biology and ecology of potential microorganisms is vital for the selection process of effective biocontrol agents and their success in controlling weeds (Sheppard 2003).

Identification of fungi with biocontrol potential is of utmost importance (Marohasy 1997). Some fungi are highly-specific on their hosts and non-toxic to the environment (Friesen et al. 2008). They continuously reproduce as long as the environmental conditions are favorable. Because of this continuous action, the cost of application of fungi as a biocontrol agent is low (Thambugala et al. 2020). Several studies suggested that one of the best strategies to identify potential fungi is to discover the natural disease agents of the targeted weed in its natural habitat (Forno & Purcell 1997). These pathogenic fungi are capable of reducing or killing the targeted weed population in a particular environment. For example, the annual release of rust *Puccinia canaliculata* has significantly controlled the yellow nutsedge in Salisbury, England (Beste et al. 1992). Following this discovery, the capability of that selected fungi to control the weed population needs to be assessed. There are several criteria to screen effective biocontrol agents. The potential agent must be adapted to the new environment, capable of establishing and maintaining a sufficient population size in the new environment, and have the capability to cause significant damage to the targeted weed (McFadyen 2003). Some examples of successful fungal biocontrol agents are also shown in Table 1.

Many plant-associated bacteria have the potential for biocontrol (Harding & Raizada 2015). For example, *Pseudomonas fluorescens* isolated from the rhizosphere of wild radish inhibit the growth of targets weeds (Flores-vargas & O'hara 2006). Bacteria isolated from plant tissues were also found to be effective as biocontrol agents (Eljounaidi et al. 2016, Widiantini et al. 2017, Morales-Cedeno et al. 2021). Deleterious rhizobacteria are important in biocontrol as they suppress weed density by limiting seed production (Kremer & Kennedy 1996). *Xanthomonas campestris* is regarded as a potential biocontrol agent to control annual bluegrass. The timing and rates of application are important factors to obtain the maximum controlling activity of *X. campestris* (Johnson et al. 1996). The bacterial pathogen, *Pseudomonas syringae* pv. *tagetis* is famous for phytotoxin production, which causes apical chlorosis in infected plants. This pathogen is common on *Asteraceae*. The studies showed that this bacteria pathogen showed more significant controlling effects on annual weeds than perennial weeds (Lydon et al. 2011).

In addition to these bacteria, many fungi are used as biocontrol agents against weeds. For example, *Sphaceloma* spp. form lesions on the lining stems and leaves of *Euphorbia hirta*, leading to plant death (Barreto & Evans 1998). Moreover, Vargas-Gaete et al. (2019) reported the successful use of *Phragmidium violaceum* against *Rubus ulmifolius*. Barton et al. (2007) highlighted the use of *Entyloma ageratinae* as one of the most successful biocontrol agents against mistflower. The infection of *E. ageratinae* starts from the bottom of the plant and spreads to the upper plant parts. After the infection spreads, leaves and stems die off. Rust and smut fungi are well-known for their adverse actions on certain weeds; hence used successfully in some biocontrol programs (Hasan & Wapshere 1973, Ellison et al. 2008, Winston et al. 2014, Hershenhorn et al. 2016, Tóth et al. 2018). Success stories of these biocontrol fungi against weeds include *Puccinia condrillina* against skeleton weeds (Hasan & Wapshere 1973), *Puccinia lagnophorae* against common groundsel and *Puccinia xanthii* against cocklebur (Tóth et al. 2018). Interactions between weeds and arbuscular mycorrhizal fungi (AMF) are widely reviewed by many scientists (Jordan et al. 2000, Rinaudo et al. 2010, Veiga et al. 2011). The influence of AMF on the composition of the weed community and the diversity of fungal species are recently well studied. In addition, soil biotic interactions affect weed biology and are important as a sustainable approach for weed management. Many weeds have a ruderal lifestyle and colonize agroecosystems (Jordan et al. 2000). Different weeds have various responses to different AMFs. Some arbuscular mycorrhizal fungi have the ability to suppress the growth of one weed and promote it in another (Al-Askar & Rashad 2010, Rinaudo et al. 2010, Olowe et al. 2018). Interactions between weed and AMFs shift from highly mutualistic to antagonistic, resulting in the reduction of plant growth (Klironomos 2003). The negative effects of AMFs on weeds are caused by several plant defense mechanisms, mainly by the production of toxic compounds by AMFs (Pigna et al. 2014). Agricultural weeds such as *Chenopodium album* and *Echinocloa crusgalli* were suppressed by AMFs (Rinaudo et al.

2010). However, understanding the effects of AMFs on individual weed species is still required for further development.

The use of plant-parasitic nematodes is also one of the alternatives to chemical herbicides. The nematode *Nothanguina phyllobia* can be found on the weed *Solanum elaeagnifolium*. Foliar galls containing *N. phyllobia* larvae formed within 10 weeks after spraying on the host plant. They significantly reduce the apical growth of the host plant and the total density of plants. Moreover, this nematode is highly specific for *S. elaeagnifolium* (Robinson et al. 1978).

Insects are also important in controlling weeds as suppression of the weed community is achieved by introducing host-specific insects (Kluge 1999). *Salvinia minima* is a free-floating aquatic fern native to South America. The weevil (*Cyrtobagous salviniae*) was released to various sites with *S. minima* in Louisiana and confirmed its use as a successful biocontrol agent against *S. minima*. The application of *C. salviniae* resulted in a significantly increased number of damaged terminal buds and decreasing total biomass of *S. minima* in Gramercy, Louisiana (Parys & Johnson 2013).

Kruess (2002) evaluated the relationships between the weed *Cirsium arvense* and its two natural enemies (fungus-pathogen and a herbivorous beetle). A cage experiment and dual-choice tests were two of the experiments that were carried out and concluded that *Phoma destructiva* and *Cassida rubiginosa* could influence *C. arvense* through indirect contact (Kruess 2002).

All the organisms (bacteria, viruses, fungi, insects, and nematodes) mentioned above are considered potential biocontrol agents for weeds. However, more research is needed to explore the effective agents to control different weed species and to understand their interactions. We also listed the other potential biocontrol agents in Table 1.

Successful case studies for using fungi in biocontrol of weed

There have been many pieces of evidence for rust fungi playing an important role in weed biocontrol (Ryan & Eliison 2003, Sankaran et al. 2008, Ellison et al. 2008, Day et al. 2013, Kumar et al. 2018, Day & Riding 2019). Here, we present some case studies of successful applications of fungal biocontrol programs that use different organisms, such as *Puccinia spegazzinii*, *Puccinia abrupta* var. *partheniicola, Puccinia rapipes, Uromyces pencanus.*

Puccinia spegazzinii* as a biocontrol agent against *Mikania micrantha

It is reported as microcyclic (the lifestyle of rust fungi that produce only the telial stage) and autoecious (rust fungi which complete the entire life cycle on one species or host). *Mikania micrantha*, a neotropic perennial vine, is native to Mexico and Argentina. This weed is a major invasive species in many parts of the world. Therefore, researchers focus on searching for potential biocontrol agents against *M. micrantha* (Ellison & Cock 2017, Kumar et al. 2018, Day & Riding 2019).

In 2005, *Puccinia spegazzinii* was released in India to control *M. micrantha*. A pathotype of the rust fungus, *P. spegazzinii* collected from Trinidad was screened for potential biocontrol activities against *M. micrantha*. The results showed that *M. micrantha* infects younger weeds, giving rise to telia and teliospores, and older weed tissues were less susceptible. The fungus infects all vegetative parts of the weed (leaves, stems and petiole) by causing necrosis, cankers and eventually death. *Puccinia spegazzinii* is host specific and infects only a few species within the genus *Mikania,* (*M. micrantha*, *M. natalensis*, *M. capensis*, *M. microptera*, *M. cordata*). It infects within a broad range of temperatures (between 15 and 25°C) after less than 10 h of exposure to free water (Ellison et al. 2008).

***Puccinia abrupta* var. *partheniicola* as biocontrol agent against *Parthenium* Weed**

Puccinia abrupta var. *partheniicola* was investigated for its biocontrol ability against *Parthenium* weed at different growth stages. The research was carried out in Central Queensland (Fauzi 2009). The study showed that rust suppresses the vegetative and generative growth of the weed. The weed is most susceptible to infection at the rosette growth stage than the flowering or mature growth stage. As a result, the final plant height was reduced by up to 22%, the reduction in the above-ground biomass reached up to 48% and the seed production was decreased by up to 90%. The study demonstrated a prominent reduction in plant height, ground biomass and seed production. Finally, the long-term reduction in seed production led to a decrease in the density of the weed population in Central Queensland (Fauzi 2009).

Puccinia rapipes as biocontrol agent against *Lycium ferocissimum*

Lycium ferocissimum is native to South Africa and is considered a widely invasive species in Australia and New Zealand. The fungus, *Puccinia rapipes* is a macrocyclic (the life cycle of rust fungi which produces five different spores; spermatia, aeciospores, urediniospores, teliospores and basidiospores) and autoecious rust. Field surveys were carried out in the Eastern and Western Cape provinces of South Africa. The suitability of *P. rapipes* as a biocontrol agent for *L. ferocissimum* in Australia was assessed using a streamlined agent selection framework (Ireland et al. 2019).

The pathogenicity was tested on *L. ferocissimum* and seven other species in the *Solanaceae* in Australia. Four species (*L. ferocissimum*, *L. barbarum*, *L. chinense*, *L. ruthenicum*) were susceptible to *P. rapipes*. *Hyoscyamus albus, H. aureus, S. aviculare, L. australe* were resistant to *P. rapipes*. According to observations, the targeted weed *L. ferocissimum* showed high susceptibility to the fungus *P. rapipes* (Ireland et al. 2019).

Potential biocontrol agents for *Euphorbia heterophylla* and *E.hirta*

Euphorbia heterophylla and *Euphorbia hirta* are native to South America. It is reported that both *Uromyces euphobiae* and *Botrytis ricini* infect *E. heterophylla* and *E. hirta* (Barreto & Evans 1998). Three fungal pathogens (*Alternaria euphorbiicola, Bipolaris euphorbiae, Sphaceloma poinsettiae*) are recorded on *E. heterophylla* (Barreto & Evans 1998, De Nechet et al. 2004, 2006). On *E. hirta*, *Colletotrichum gloeosporioides*, *Sphaerotheca fuliginea* and *Sphaceloma manihoticola* have been reported as pathogens (Barreto & Evans 1998).

During this survey, *U. euphorbiae* caused severe damage to photosynthesis and the reproductive tissues of host weeds. *Alternaria euphorbiicola* showed symptoms, such as stem necrosis, defoliation and cankers, but was unable to survive at low temperatures and under heavy rainfall (Barreto & Evans 1998, Varejão et al. 2013). *Bipolaris euphorbiae* has potential mycoherbicide activity when applied during the early season because infections occur when the weeds mature and have produced viable, long-lived seeds. Now, mycoherbicides from *B. euphorbiae* have been developed in Brazil (Barreto & Evans 1998).

Sphaerotheca fuliginea also has the potential to control *E. hirta* as it causes severe defoliation during winter and is difficult to keep mildew-free stands of the weeds in the greenhouse (Barreto & Evans 1988, Milod et al. 2021). *Sphaeceloma poinsettiae* is a potential biocontrol agent for *E. heterophylla*. Severe infection by *S. poinsettiae* leads to weed death due to coalesce and girdle stems. It also inhibits flowering, fruiting, and stem elongation, and the infection is more cryptic in older weeds (Barreto & Evan 1988, De Nechet et al. 2004). *Sphaeceloma manihoticola* is a potential biocontrol agent for *E. hirta*. Infections caused by these two *Sphaceloma* species not only weaken the hosts (*E. heterophylla* and *E. hirta*) but also kill the hosts (Barreto & Evans 1998). *Colletotrichum gloeosporioides* is not suitable for the biocontrol of *E. heterophylla* and *E. hirta* because it requires a high humidity level to cause a high level of host damage (Barreto & Evans 1998). The research provides many fungal pathogens, which have mycoherbicidal potential but still need further studies using a combination of these fungi for efficient biocontrol (Barreto & Evans 1998).

Uromyces pencanus as biocontrol agent against *Nassella neesiana*

Nassella neesiana is native to South America but widespread in many parts of the world. *Nassella neesiana* becomes a target for biocontrol in Australia and New Zealand (Anderson et al. 2010). Three fungal pathogens (*Uromyces pencanus*, *Puccina nassellae*, and *P. graminella*) are regarded as potential biocontrol agents for *N. neesiana* (Anderson et al. 2006, 2010, 2011). Among them, *U. pencanus* has the most promising effect on target weed populations. After collecting *U. pencanus* isolates from *N. neesiana* in Argentina for five years, it was introduced into Australia and New Zealand for biocontrol programs. *Uromyces pencanus* is a biotrophic, autoecious fungus that causes significant damage to *N. neesiana*. Infected plants showed serious symptoms, such as intense chlorosis and chronic energy uptake from their host. Moreover, they inhibit seed production and reduce the competitive ability of *N. neesiana* (Anderson et al. 2010).

Table 1 List of some fungal biocontrol agents and their target weeds.

Fungal biocontrol agents	***Target weeds***	***References***
Bipolaris euphorbiae	*Euphorbia heterophylla*	De Nechet et al. (2006)
Cercospora pistiae	*Pistia stratiotes*	Barreto (1998)
Entyloma ageratinae	*Ageratinae riparia*	Barreto & Evans (1988)
Lasiodiplodia pseudotheobromae	*Amaranthus hybridus* L. (pigweed)	Adetunji et al. (2017)
Phragmidium violaceum	*Rubus fruiticosus*	Bruzzese & Field (1985)
Plectosporium alismatis	*Sagittaria montevidensis*	Lima et al. (2010)
Puccinia abrupta	*Parthenium hysterophorus*	Parker et al. (1994)
Puccinia carduorum	*Carduus thoermeri* (Must thistle)	Baudoin et al. (1993)
Puccinia chondrillina	*Chondrillina juncea* (Skeleton weed)	Hasan & Wapshere (1973)
Puccinia jaceae	*Centaurea diffusa*	Mortensen et al. (1991)
Secusio extensa	*Senecio madagascariensis* (Fireweed)	Assessment et al. (2008)
Uromyces galegae	*Galega officinalis*	Tunali et al. (2006)
Uromyces heliotropii	*Heliotropium europaeum*	Hasan & Aracil (1991)
Uromyces pencanus	*Nassella neesiana*	Anderson et al. (2010)
Uromycladium tepperianum	*Accacia saligna*	Morris (1987)
Cercospora pistiae	*Euphorbia heterophylla*	De Nechet et al. (2006)

Overview of mycoherbicides

The use of mycoherbicides is an inundative approach in weed biocontrol. In this approach, pathogenic fungi are already present (native or introduced), and their population is artificially increased by mass rearing (Patel & Patel 2015). Mycoherbicides reduce the weed population by exploiting natural metabolites produced by microorganisms, especially fungi (Dagno et al. 2012, Berestetskiy & Sokornova 2018, Dalinova et al. 2020, Zarafi & Marley 2021).

In the classical approach, biocontrol agents are released into weed populations and spread naturally in that community (Howarth 1983, Reznik 1996, Harris 1991, Hinz et al. 2020). The increase of diseases in weeds reduces the production of their seeds and affects plant survival (Schwarzländer et al. 2018). The bioherbicide approach focuses on the use of pathogens that naturally occur in native communities (indigenous), artificially increase the level of organisms and apply directly to targeted weeds (Jackson et al. 1996, Bailey 2014, Hallett 2005, Boyette et al. 2016). The process of mycoherbicide production is as follows: fungal pathogens are grown in laboratories, produced in mass quantities, and formulated into standardized products (Boyette et al. 1991, Berestetskiy & Sokornova 2018). The formulation and application of mycoherbicides are similar to chemical herbicides. One of the objectives of using mycoherbicides is to reduce the input amount of chemicals to provide effective weed biocontrol (Watson 1993).

However, many pathogens with the potential for mycoherbicides need further studies as it is important to know the level of aggressiveness needed to overcome the weed defense mechanisms and the level of the pathogen's ability to control targeted weed species.

Mycoherbicides are usually applied as spores suspended in a liquid, however, it is not the most effective form. The initial, most favorable formulation for mycoherbicide is the wettable powder comprised of a hydrophilic carrier mixed with hydrophobic spores (Evans et al. 2001), allowing the spores to survive more than two years without losing their viability and efficacy.

Mycoherbicide production is a long-term process from organism selection to commercial distribution. Formulations of mycoherbicides are important for their effectiveness (Boyette et al.

1991). Low-cost production methods facilitate the successful commercial production of mycoherbicides. Another important characteristic of commercial mycoherbicides is the ability of their propagules to survive in long-term storage conditions (Berestetskiy & Sokornova 2018). The commercially available mycoherbicides and their target weeds are listed in Table 2.

Table 2 List of mycoherbicides and their target weeds.

Mycoherbicide	Pathogen	Formulation	Target	Remark	Reference
DeVine	*Phytophthora palmivora*	Liquid formulation mixed with fungal chlamydospores	*Morrenia odorata* (milkweed vine)	sprayed to the soil during the active growth of the weed	Feichtenberger et al. (1984)
Collego	*Colletotrichum gloeosporiodes*	Liquid formulation	Northern Jointvetch (*Aeschynomene virginica*)	applied once in a season in July or August	Templeton (1984)
BioMal	*Colletotrichum gloeosporioides* f. sp. *malvae*	Solid formation	*Malva pusilla*	During application, the spore materials are suspended in water and sprayed on the plants	Makowski & Mortensen (1990)
CASST	*Alternaria cassia*	Liquid formulation	*Cassia obtusifolia* (sicklepod)	Spraying mixture containing 5×104 or more conidia/ml showed maximum control	Walker &Riley (1982)

Factors that affect mycoherbicide efficacy

Mycoherbicides reveal more variations depending on their target weeds than synthetic herbicides. Many factors that affect the efficacy of mycoherbicides are discussed in several studies (Yang & TeBeest 1993, Daigle & Cotty 1994, Boyette et al. 1996, Boyetchko & Peng 2004, Boyette et al. 2018). Mycoherbicide efficacy is mainly affected by environmental factors, which can influence the ability to sporulate in formulations of mycoherbicides (Klein & Auld 1995). When these mycoherbicides are applied in the field, environmental conditions such as dew period, temperature, and moisture availability immediately become hostile for the biocontrol agents (Boyetchko & Peng 2004). In some cases, low-temperature conditions extend the duration of the dew period and provide favorable conditions for fungal infection. It has been reported that more than 12hrs of the dew period is required for the pathogenic fungus to cause the infection, and is the most important constraint for the success of mycoherbicides. Moisture is more important than the temperature for the efficacy of mycoherbicides (Boyetchko & Peng 2004). For example, some species, such as *Colletotrichum orbiculare*, require high temperatures for controlling *Xanthium spinosum* (Auld et al. 1988).

Techniques and conditions involved in the cultivation of biocontrol agents and selection of nutrient media are important to reach high biomass and also to determine their efficacy in the field. Fungal propagules (conidia, mycelium, sclerotia, etc.) can be produced by solid-state or liquid fermentation or in both phases. Generally, high spore density is required for mycoherbicides to use in field conditions (Berestetskiy & Sokornova 2018). The nutrient composition, such as carbon concentration and carbon to nitrogen ratio (C/N) influence the sporulation of fungi in mycoherbicide formulations. For example, conidia of *Colletotrichum truncatum* were formed in media with different C/N ratios of 80:1, 30:1, and 10:1. According to the results, all these conditions caused a reduction in the biomass of seedlings in *Sesbania exaltata*. Conidia produced on the 10:1 or 30:1 medium showed a greater reduction in shoot height and dry weight than conidia from the 80:1 medium (Schisler et al. 1991).

The stabilization of fungal propagules is one of the factors that influence mycoherbicide efficacy. For commercial mycoherbicide production, microorganisms need to be stabilized to prevent the germination of their propagules during their long storage period. This condition is manipulated by lowering the pH, temperature, oxygen concentration and water activity (Berestetskiy & Sokornova 2018).

Mode of action of mycoherbicides

The mode of action of mycoherbicides determines the compatible interactions between the host weed and the pathogen (Yang & TeBeest 1993, Swain & Mukherjee 2020). This also influences the success of the infection. These mycoherbicides act on the weeds by producing several enzymes or phytotoxic secondary metabolites (Vurro et al. 2018, Dubovik et al. 2020, Di Lecce et al. 2020, Xu et al. 2021). Many fungal-derivative enzymes (celluloses, liginases and peptidases) are important for plant cell wall degradation. Moreover, proteinases, peptidases, amylases and phospholipases degrade protein and lipid membranes, which will facilitate the infection of the biocontrol agent on the targeted weed (Goodwin 2001, da Costa et al. 2021, Peng et al. 2021).

The mode of action of mycoherbicides explains the mechanism used by these phytotoxic secondary metabolites to interfere with the plant metabolism (Fletcher & Kirkwood 1982, Devine et al. 1992, Cobb & Reade 2011). Many hemibiotrophic fungi are the target agents for mycoherbicide production. For example, *Colletotrichum gloeosporioides* was developed as an effective mycoherbicide to control round-leaved mallow, *Malva pusilla* (Grant et al. 1990). *Colletotrichum gloeosporioides,* an intracellular hemibiotroph, feeds biotrophically on host cells and then continues necrotrophic growth (Wei et al. 1997, Perfect et al. 1999). During necrotrophic growth, harmful toxic metabolites are produced and cause plant death. The study showed the importance of the infection process (penetration, biotrophy, and necrotrophy) for disease virulence on *M. pusilla* and highlighted the molecular basis of weed-mycoherbicide interaction.

Fungal phytotoxins play an important role in inducing disease symptoms (Masi et al. 2018, Evidente et al. 2019, Cimmino et al. 2020). They belong to different classes of naturally occurring compounds, such as pyrones, ethanones, furopyrans, cytochalasins, nonenolides, aromatic, amino acids, coumarins, isocoumarins, spirophytotoxins, terpenes and many others (Cimmino et al. 2015). Here, we provide some examples of fungal phytotoxins and their mode of action on weeds. Many phytotoxins produced by co-evolved fungi are host-specific and usually considered safe mycoherbicides. For example, Cyperin is a natural mycotoxin produced by several fungal pathogens like *Preussia fleischhakii, Phoma sorghina* and *Ascochyta cypericola* (Vurro 2007, Duke & Dayan 2011). According to Cimmino et al. (2015), a high concentration of cyperin will inhibit protoporpbyrinogen oxidase activity and cause loss of membrane integrity in dark conditions. The most significant result of this infection is the growth inhibition shown by the decreased root length of the weed. This inhibition activity depends on the dose of application.

Another example is the vulculic acid produced by *Nimbya alternantherae* that damages the alligator weed, *Alternanthera philoxeroides* (Chen et al. 2010, Xiang et al. 2008, 2013, Li et al. 2012). The mode of action of vulculic acid is well studied. It acts as a photosynthetic inhibitor and damages photosystem I and II proteins. Its major targets are the O_2 evolving complex and light-harvesting complex on the photosystem II donor side (Cimmino et al. 2015).

Phoma macrostoma also controls some weeds, such as *Cirsium arvense* (Canada thistle) and *Taraxacum officinale* (Dandelion). Its phytotoxic secondary metabolite, macrocidins, has an impact on the carotenoid biosynthesis of weeds and inhibits the carotenoid biosynthetic enzyme, phytoene desaturase (PDS) (Hubbard et al. 2015).

Conclusions and future perspectives

In this study, we reviewed the use of various organisms that have the potential for controlling weed species. Fungi are also among the most effective biocontrol agents for weeds. Moreover, fungi are the most promising tools in weed control because they can reduce the risks of environmental problems. Aside from the traditional approach, mycoherbicides should be considered a top priority for achieving sufficient virulence against weeds. There are some limitations and challenges for the production of successful commercial products. For developing successful commercial mycoherbicides, initial field experiments should be carried out under different environmental conditions. Consistent efficacy (in mass inoculum production and under field conditions) is essential to achieve long-term commercial success. The limitations discussed in this review are the reasons for the decline in the number of commercial mycoherbicides. Moreover, the use of saprobic fungi in biocontrol is a need for future researchers. Although there are some studies on the saprobes with potential biocontrol capabilities (Botrel et al. 2018), the role of saprobic fungi in biocontrol still needs to be explored further as reports of saprobic fungi in biocontrol are rare. Many rules and regulations should be established by governments to enhance the application of mycoherbicides in sustainable agriculture. However, the integration of different methods proved to be more effective and economical. Hopefully, this will help to build a better agroecosystem, leading to a greener world by reducing chemicals and improving the quality of crops.

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